Impact of dispersal on the stability of metapopulations

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Abstract

Dispersal is a key ecological process, that enables local populations to form spatially extended systems called metapopulations. In the present study, we investigate how dispersal affects the stability of a general metapopulation model. We find that dispersal impacts the stability of metapopulations through local patches dynamics and various dispersal behaviors (positive density-dependent dispersal, costly dispersal, social fencing of immigrants and settlement facilitation). We also show that in homogeneous metapopulations, a density-independent dispersal does not affect stability, whereas in heterogeneous ones it can yield an impact on stability, that is modulated by the spatial structure of the metapopulation.

Introduction

Spatial structure is an important factor in ecological systems. Many species occupy a system of patches that are linked together by dispersal, forming a spatial network called a metapopulation. Understanding the dynamics of metapopulations is essential for deciding which metapopulation spatial structure should be preserved or created, in order to allow for the persistence or the establishment of a specific species. Untangling the influence of dispersal on the stability and the structure of metapopulations is then a challenge in metapopulation biology.

It has been shown that dispersal can affect the stability of a metapopulation through various dispersal behaviors. Bascompte & Solé found that increasing density-independent dispersal can destabilize metapopulations [2], whereas Hassel *et al.* [10], followed by Rohani *et al.* [18] and Jang & Mitra [13], concluded that it does not influence the stability of metapopulations. Further, it has been shown that under certain conditions, density-dependent dispersal can be destabilizing [20, 25, 24]. By contrast, it has been argued that a weak coupling between chaotic patches can stabilize the whole metapopulation [19, 27] and Ruxton *et al.* subsequently found that costly migration can stabilize metapopulations [22, 21]. This result has been questioned by Kisdi

[14], who shows that costly dispersal can also have a destabilizing influence on metapopulation dynamics, using a specific growth function.

The previous theoretical studies are based on models using specific functional forms, such as the Hassel growth function [9, 10]. This restriction of the kinetics in the model is necessary to obtain certain results, such as steady state values. However, it is essential to ask in which way the results that have been reported are contingent on the assumption of the specific kinetic laws. For example, it has been shown that results concerning the paradox of enrichment in trophic systems are strongly dependent on the specific functional forms used [6].

Other assumptions are frequently made in order to analyse the stability of metapopulations. Because metapopulations lead to high dimensional dynamical systems, previous mathematical studies typically reduced their complexity by assuming that dispersal is symmetric or patches are identical. The influence of growth rate heterogeneity between patches has been investigated by Dey *et al.* [3], who found that it does not affect stability, even with different topologies.

Here, we investigate the stability of metapopulations using a generalized modeling approach. We introduce a general metapopulation model, which does not assume specific kinetic laws, and encompasses both homogeneous and heterogeneous cases. In the homogeneous case, all patches are identical (as in [22]), whereas in the heterogeneous case, parameters may differ between patches [3, 28]. The homogeneous case enables us to draw analytical conclusions on the influence of dispersal behaviors such as density-independence, positive density-dependence and costly dispersal on metapopulation stability, but also of less studied behaviors such as social fence and social facilitation. Investigation of heterogeneous webs shows that the influence of density-independent dispersal on stability is not neutral, but strongly dependent on the topology of the metapopulation.

Model

We consider a metapopulation consisting of M patches and denote the population density in patch i as X_i. The dynamics of that metapopulation can then be described by the following set of general differential equations:

$$\dot{X}_i = G_i(X_i) - M_i(X_i) + \sum_{k=1}^{M} I_{i,k}(G_k(X_k)), \tag{1}$$

where G, M, and I denote potentially non-linear functions governing the local growth, loss and immigration rates in the respective patches. Specifically, we distinguish between different immigration terms $I_{i,k}$ originating from different source patches $k \neq i$.

Note that immigration is assumed to depend on the growth rate of the donor patch and not on its density. This choice is directly intuitive for a population with distinct life stages, where only a proportion of the juveniles migrates to other patches. In this case immigration is directly dependent on the number of juveniles in the donor patch. Furthermore, juveniles leaving before reaching adulthood do not need to be accounted for in the donor patch and hence there is no associated loss rate.

We note that Eq. 1 remains applicable in a much wider class of settings. Because we do not restrict the functional forms of G, M, and I, letting the immigration rate depend on G rather than X does not reduce the generality as long as G is a reversible function, which is

quite generally the case. Similarly any loss arising from emigration can be accounted for in the function M.

We note furthermore that considering a population with distinct juvenile and adult life stages enables to segregate competition and dispersal, in accordance with Hassel's criticism of Bascompte & Solé model [2, 10].

The generalized model from Eq. 1 describes a whole class of conventional models, in which the functions G, M and I are restricted to specific functional forms. Clearly, many of these conventional models will have steady states in which the abundances of species remain stationary. In the following we identify conditions that govern the stability for all positive steady states in all models within the class considered here. For this purpose we denote the biomass densities in an arbitrary steady state by $(X_1^*, X_2^*, ..., X_M^*)$, and define the normalized variables

$$x_i := \frac{X_i}{X_i^*}, \tag{2}$$

and the normalized functions

$$g_i(x_i) := \frac{G_i(X_i^* x_i)}{G_i^*} \quad , \quad m_i(x_i) := \frac{M_i(X_i^* x_i)}{M_i^*} \quad , \quad \eta_{i,k}(x_k) := \frac{I_{i,k}(G_k(X_k^* x_k))}{I_{i,k}^*}, \tag{3}$$

where we use an asterisk $(*)$ to denote the values that the functions assume in the steady state X^*. Normalized variables and functions are thus equal to 1 at the steady state. We can now rewrite our model in terms of the normalized variables and functions, by substituting the definitions Eqs. (2) and (3) into Eq. (1). We obtain

$$\dot{x}_i = \frac{G_i^*}{X_i^*} g_i(x_i) - \frac{M_i^*}{X_i^*} m_i(x_i) + \sum_{k=1}^{M} \frac{I_{i,k}^*}{X_i^*} \eta_{i,k}(g_k(x_k)) \tag{4}$$

The prefactors appearing in this equations are unknown constants and therefore can be interpreted as unknown parameters of the model. We define

$$\alpha_i := \frac{G_i^*}{X_i^*} + \sum_{k=1}^{M} \frac{I_{i,k}^*}{X_i^*} = \frac{M_i^*}{X_i^*} \quad , \quad \nu_i := \frac{G_i^*}{G_i^* + \sum_{k=1}^{M} I_{i,k}^*} = \frac{1}{\alpha_i} \frac{G_i^*}{X_i^*}$$

$$\tilde{\nu_i} := 1 - \nu_i = \frac{\sum_{k=1}^{M} I_{i,k}^*}{G_i^* + \sum_{k=1}^{M} I_{i,k}^*} = \frac{1}{\alpha_i} \sum_{k=1}^{M} \frac{I_{i,k}^*}{X_i^*} \quad , \quad \theta_{i,j} := \frac{I_{i,j}^*}{\sum_{k=1}^{M} I_{i,k}^*} = \frac{1}{\alpha_i \tilde{\nu_i}} . \frac{I_{i,j}^*}{X_i^*}$$

These parameters all denote densities and biomass fluxes in the system at the equilibrium and are easily interpretable in the context of the model; in accordance with [5], we call them *scale parameters*. The parameter α_i is the biomass turnover rate of individuals in patch i. As a characteristic timescale of the species, it is always positive. The parameter ν_i represents the fraction of growth in patch i resulting from production, whereas $\tilde{\nu_i}$ denotes the fraction of growth in patch i resulting from immigration. These parameters thus encode the impact of dispersal on growth in each patch at the steady state. We can assume $\tilde{\nu}$ to be close to 0 in self-sustaining patches, whereas $\tilde{\nu}$ is close to 1 in patches where the population can only be maintained by strong immigration. The parameter $\theta_{i,j}$ denotes the relative weight of contribution of individuals from patch j to the immigration to patch i. For example, in the case of a n patches metapopulation, if immigrants to patch number n are equally composed of emigrants from all the other patches,

Table 1: List of GM parameters used in the model

Parameter	Interpretation	Simulation value (heterogeneous case)
Scale parameters		
α_i	Rate of biomass turnover in patch i	1
ν_i	Fraction of growth due to production in i	$1-\tilde{\nu}_i$
$\tilde{\nu}_i$	Fraction of growth due to immigration in i	$\{0.1, 0.3, 0.7, 0.9\}$
$\theta_{i,j}$	Relative weight of j in the gain from immigration of i	$\frac{I_{i,j}}{\sum_k I_{i,k}}$
Exponent parameters		
ϕ_i	Sensitivity of primary production to density in i	$\in [0, 2]$
μ_i	Sensitivity of loss to density in i	1
$\omega_{i,j}$	Sensitivity of immigration in i to the density in the donor patch j	1
$\zeta_{i,j}$	Sensitivity of immigration in i to the density in the recipient patch i	0

we have $\theta_{n,k} = 1/(n-1)$ for all $k < n$. In the following we consider that the set of variables $\theta_{i,j}$ defines the topology of the metapopulation.

Using the newly defined parameters we can write the generalized model as

$$\dot{x}_i = \alpha_i \big[\nu_i g_i(x_i) - m_i(x_i) + \tilde{\nu}_i \sum_{k=1}^{M} \theta_{i,k} \eta_{i,k}(g_k(x_k))\big] \tag{5}$$

To study the stability of the steady state, we calculate its Jacobian matrix at the equilibrium under consideration. The Jacobian matrix constitutes a local linearization of the system and contains derivatives of the normalized functions with respect to the state variables, evaluated at the equilibrium. Again these derivatives are unknown constants and can thus be considered as additional parameters of the system, that we call *exponent parameters*. The exponent parameters are defined as

$$\phi_i := \left.\frac{\partial g_i(x_i)}{\partial x_i}\right|_{x=x^*} \quad , \quad \mu_i := \left.\frac{\partial m_i(x_i)}{\partial x_i}\right|_{x=x^*}$$

$$\zeta_{i,k} := \left.\frac{\partial \eta_{i,k}(g_k(x_k))}{\partial g_i}\right|_{x=x^*} \quad , \quad \omega_{i,k} := \left.\frac{\partial \eta_{i,k}(g_k(x_k))}{\partial g_k}\right|_{x=x^*} .$$

It can be shown that the exponent parameters measure the so-called elasticity of rate-laws in the steady state. Elasticities where originally proposed in economy as a measure of nonlinearity of a function [17]. They have the advantage of allowing a particularly easy comparison with experimental data, and are now also widely used in metabolic control theory [4]. They thus provide a nonlinear measure for the sensitivity of the functions to variations in the variables at the steady state. For instance, power-law functions of the form aX^p have a constant elasticity which is equal to p - the elasticity of a linear function is 1 and that of a quadratic function is 2. For more complex functions, the value of the elasticity is not constant, and depends on the steady state. For instance for a Holling type-II functional response, the elasticity (with respect to prey) is 1 (linear) at low prey density and 0 (constant) close to saturation.

In the model, the parameter ϕ_i denotes the sensitivity of primary production in patch i to the density of individuals. In populations that do not suffer from resource limitation, we would expect that production increases locally linearly with population size and thus that $\phi_i = 1$. If social facilitation leads to an increase in productivity (a weak Allee effect [29]), then even a superlinear increase in production with population size ($\phi_i > 1$) can be observed. But overcrowding can lead to a competition for resources, where the increase in production with population size becomes sublinear ($\phi_i < 1$) and it can even result in a negative density-dependent production ($\phi_i < 0$).

The parameter μ_i denotes the sensitivity of the loss rate to the density of individuals in patch i. In populations that suffer from resources limitation, it can be expected that losses increase superlinearly with density ($\mu_i > 1$), or that this increase is limited by social facilitation ($\mu_i < 1$).

The parameters $\zeta_{i,k}$ and $\omega_{i,k}$ encode information on dispersal behaviors. The parameter $\omega_{i,k}$ denotes the sensitivity of immigration to the donor patch growth rate. Hence, when dispersal is density-independent, we would expect that immigration increases linearly with production, and thus that $\omega_{i,k} = 1$. When patches are subject to resource competition, positive density-dependent migration can be observed, where emigration is enhanced by overcrowding [16]; in this case, we would expect the sensitivity of immigration to density in the donor patch to be superlinear ($\omega_{i,k} > 1$). Resources depletion can also impede the success of migration when

Table 2: Behavioral interpretation of the values of exponent parameters

Elasticity value	Corresponding behavior
$\phi > 1$	positive density-dependent production (weak Allee effect)
$\phi < 1$	competition for resources
$\phi < 0$	negative density-dependent production
$\mu > 1$	positive density-dependent loss
$\mu < 1$	social facilitation
$\omega = 1$	density-independent emigration
$\omega > 1$	positive density-dependent dispersal
$\omega < 1$	costly dispersal
$\zeta = 0$	density-independent immigration
$\zeta > 0$	settlement facilitation
$\zeta < 0$	social fence against immigrants

dispersal is energetically costly [22]; the sensitivity of immigration to the donor patch density would then become sublinear ($\omega_{i,k} < 1$).

The parameter $\zeta_{i,k}$ denotes the sensitivity of immigration to the growth rate in the recipient patch. When density inside the host patch has no influence on the settlement of immigrants [15], immigration can be regarded as density-independent ($\zeta_{i,k} = 0$). When the settlement of immigrants is facilitated by high densities in the host patch, we would expect that immigration increases with density inside the host patch ($\zeta_{i,k} > 0$) [1]. But when the settlement of immigrants is impeded by hosts, immigration would then decrease with the density inside the host patch ($\zeta_{i,k} < 0$). This latter case is similar to the social fence hypothesis, stating that when the neighbouring patches of a population reach a sufficiently high density, they socially fence immigrants out by inhibiting their settlement [11, 8].

A summary of all parameters used here is shown in Table 1, and the ecological interpretation of the elasticities can be found in Table 2. For additional discussions of generalized modelling, see [5] and [7].

Using these parameters, we write the Jacobian matrix, to study the dynamics of the system at the steady state. The diagonal elements of the Jacobian matrix are

$$J_{i,i} = \alpha_i \big[\nu_i \phi_i - \mu_i + \tilde{\nu}_i \sum_{k=1}^{M} \theta_{i,k} \phi_i \zeta_{i,k}\big], \tag{6}$$

and the non-diagonal elements are

$$J_{i,j} = \alpha_i \big[\tilde{\nu}_i \theta_{i,j} \phi_j \omega_{i,j}\big] \tag{7}$$

A given steady state is stable if all eigenvalues of the Jacobian matrix have negative real parts. A dynamical system is thus stable if the largest eigenvalue has a negative real part. To estimate this eigenvalue, we use a theorem stating that the largest eigenvalue of a Jacobian is smaller than its largest row sum, but larger than its smallest row sum [30, 13]. The row sum of the Jacobian is

$$\sum_{j=1}^{M} J_{i,j} = \alpha_i C_i, \quad \text{with} \quad C_i := \phi_i - \mu_i + \tilde{\nu}_i(\langle \phi_j \omega_{i,j} + \phi_i \zeta_{i,j} \rangle - \phi_i), \tag{8}$$

where $\langle \phi_j \omega_{i,j} + \phi_i \zeta_{i,j} \rangle = \sum_{j=1}^{M} \theta_{i,j}(\phi_j \omega_{i,j} + \phi_i \zeta_{i,j})$, i.e the mean of $\phi_j \omega_{i,j} + \phi_i \zeta_{i,j}$ weighted relatively to $\theta_{i,j}$, the relative strength of biomass flows from patch i to j. The system is stable if the largest row sum is inferior or equal to zero. A necessary condition for stability is that there is at least one row sum that is inferior or equal to zero, and a sufficient condition is that all row sums are inferior to zero. Insofar as α_i is positive, the sign of the row sum depends on C_i. These conditions allow us to determine the influence of the parameters of the model on its stability.

To calculate the influence of dispersal on stability, we compute the derivative of the row sums (C_i) with respect to the fraction of growth due to immigration $\tilde{\nu}_i$. If patch i receives migrants, this yields

$$\frac{\partial C_i}{\partial \tilde{\nu}_i} = \langle \phi_j \omega_{i,j} + \phi_i \zeta_{i,j} \rangle - \phi_i \tag{9}$$

If the ith rowsum is the largest and that $\partial C_i / \partial \tilde{\nu}_i$ is positive, then dispersal has a stabilizing influence on the system, whereas if $\partial C_i / \partial \tilde{\nu}_i$ is negative, then dispersal has a destabilizing influence. This result enables us to compute the influence of dispersal on the stability of homogeneous and heterogeneous metapopulations.

Homogeneous patches

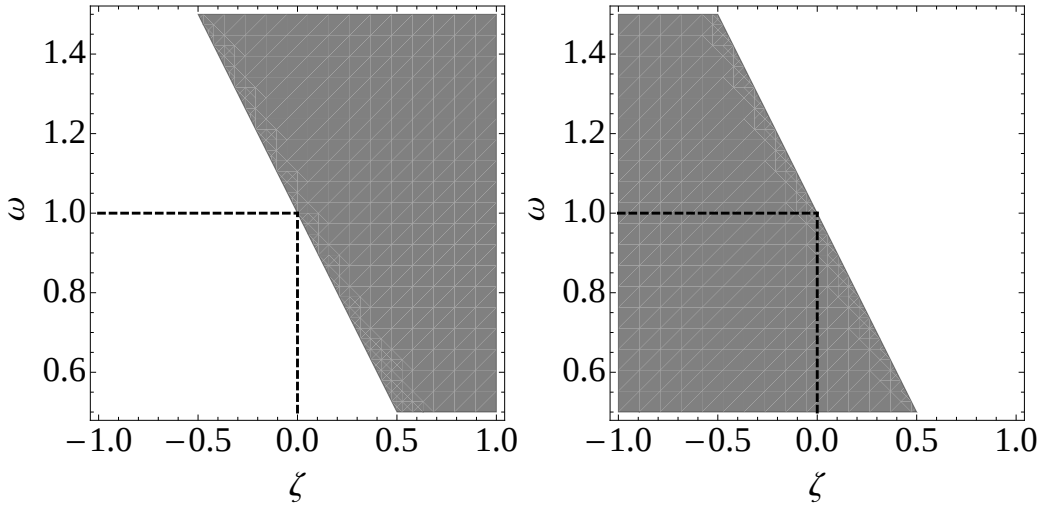
We first consider the case of homogeneous metapopulations, where all patches possess the same parameter values and are thus equivalent. All row sums are equal to $C = \alpha\big[\phi(1+\tilde{\nu}(\omega+\zeta-1))-\mu\big]$, because $\sum_{j=1}^{M} \theta_{i,j} = 1$. The largest eigenvalue is then αC (the parameter α is positive by definition).

We notice that the sensitivity of loss to density (μ) is always stabilizing, and that in absence of dispersal ($\tilde{\nu} = 0$), the sensitivity of production to density (ϕ) is always destabilizing. This confirms that a highly positive density-dependent production is destabilizing, whereas a non-linear loss stabilizes the metapopulation [7]. But in presence of immigration ($\tilde{\nu} > 0$), then ϕ is stabilizing if $\omega + \zeta < (\tilde{\nu} - 1)/\tilde{\nu}$. This implies at least one of the elasticities of dispersal (ω and ζ) to be negative. It intuitively means that a non linear production can become stabilizing when it is dampened by dispersal.

We now focus on the effect of dispersal on stability by adapting Eq. (9) to the homogeneous case. We obtain

$$\left.\frac{\partial C}{\partial \tilde{\nu}}\right|_{*} = \phi(\omega + \zeta - 1) \tag{10}$$

The dependence of the impact of dispersal on stability on the elasticities of dispersal is shown in Figure 1. It appears that when the elasticity of production is positive, increasing these parameters leads to a destabilizing dispersal (Fig. 1a), whereas when it is negative, it leads to a stabilizing dispersal (Fig. 1b). We also note that a density-independent dispersal ($\omega = 0$, $\zeta = 0$) has no effect on metapopulation stability (intersection of dashed lines in Figs. 1a and 1b). When the elasticity of production is positive (negative), we observe that costly dispersal



(a) $\phi > 0$ (b) $\phi < 0$

Figure 1: Influence of immigration on stability for homogeneous patches, in dependence on the sensitivity of immigration to the birth rate in the donor patch (ω) and in the recipient (ζ). When $\phi > 0$, immigration is stabilizing (white area) for low sensitivities, whereas it is destabilizing (grey area) for high sensitivities. When $\phi < 0$, immigration is destabilizing for low sensitivities, whereas it is stabilizing for high sensitivities. The equation $\omega + \zeta = 1$ represents the threshold between a stabilizing and a destabilizing dispersal.

($\omega < 1$) and social fence of immigrants ($\zeta < 0$) stabilize (destabilize) dispersal, whereas positive density-dependent dispersal ($\omega > 1$) and settlement facilitation ($\zeta > 0$) destabilize (stabilize) it. It also appears that the threshold between a stabilizing and a destabilizing migration depends on both elasticities of dispersal. So, the impact of dispersal on stability can be determined by the relative strength of co-occurring behaviors. For instance, a highly costly dispersal ($\omega = 0.6$) adjuncted to a high settlement facilitation ($\zeta = 0.5$) leads to a destabilizing dispersal. But if ζ shifts down a little to become inferior to 0.4, migration becomes stabilizing.

Heterogeneous patches

Let us now investigate the heterogeneous case where some parameters are allowed to vary between patches. We consider the case $\zeta_{i,j} = 0$, $\omega_{i,j} = 1$. This corresponds to density-independent dispersal, which has no influence on the stability of homogeneous metapopulations. We compute the influence of dispersal on stability:

$$\left.\frac{\partial C_i}{\partial \tilde{\nu}_i}\right|_* = \sum_{j=1}^{M} \theta_{i,j}\phi_j - \phi_i. \tag{11}$$

Thus, the conditions for dispersal to be stabilizing only depends on the values of the ϕ_i and on the $\theta_{i,j}$, which carry the information about the topology of the network. This indicates that density-independent dispersal can have an influence on stability for heterogeneous patches, and that this influence depends on the topology of the network.

In order to assess the impact of dispersal on the stability of complex heterogeneous metapopulations, we study it numerically. We first generate an ensemble of topologies by randomly placing k links between M patches, such that topologies with connectance $C = k/(M(M-1))$ are created. We then check the connectivity of the created topologies, rejecting those containing disconnected components. A randomly generated network can be represented by its adjacency Matrix $\mathbf{A}$, where A_{ij} is equal to 1 if a link from patch i to j exists, and 0 otherwise. From the random adjacencies we compute the parameters

$$\theta_{ij} = \frac{A_{ji}}{\sum_i A_{ji}} \tag{12}$$

which is consistent with the assumption that $\theta_{i,j}$ denotes the relative weight of j in the gain from immigration of i. We randomly draw ϕ_i from an uniform distribution of range $[0, 2]$, centered on 1, thus creating an heterogeneity between patches. The other elasticities are fixed, as is the fraction of growth due to immigration $\tilde{\nu}_i$ for patches that receive migrants (See Table. 1). To determine the influence of dispersal on the stability of each network, when then calculate the Jacobian matrix and the row sums by using Eq. 6 to 8 We then compute a proportion of webs for which there is a stabilizing dispersal, that we call PSD.

We observe in Fig. 2 that in randomly constructed metapopulations with density-independent migration ($\omega = 1$ and $\zeta = 0$), dispersal can be either globally stabilizing ($PSD > 0.5$) or destabilizing ($PSD < 0.5$). The correlation between the PSD and the fraction of growth due to immigration $\tilde{\nu}$ is globally negative, indicating that dispersal is more likely to be stabilizing for low intensities of immigration. We also note that dispersal is more stabilizing in complex networks, i.e when the connectance and the number of patches are high. When immigration plays a important role in growth (high $\tilde{\nu}$), dispersal is less stabilizing in small networks of high connectance, and in large networks of low connectance. We thus observe that in heterogeneous metapopulations, the relationship between dispersal and stability crucially depends on the topology of metapopulations.

Conclusions

We used generalized modeling to assess the influence of dispersal on the stability of metapopulations. This approach allowed us to derive analytical results on a broad class of homogeneous networks and to obtain detailed results on heterogeneous metapopulations. Our analysis revealed six ecological results, that are gathered in Table 3.

First, we found in accordance with most existing models that density-independent dispersal has no influence on stability. Interestingly, if we follow Bascompte & Solé assumption of not segregating reproduction and migration, i.e if the immigration term depends on the density and not on the growth rate, then $\omega_{i,j} = \partial\eta_{i,j}/\partial x_j$, $\zeta_{i,j} = \partial\eta_{i,j}/\partial x_i$. In the case of homogeneous patches that all receive migrants, the condition for a stabilizing dispersal becomes $\omega - \phi + \zeta < 0$. It is obvious that density-independent migration is then destabilizing if $\phi < 1$, i.e in the case of a growth limited by competition, which corresponds to their model at the equilibrium.

Second, we showed that a positive density-dependent dispersal is destabilizing when the sensitivity of production to density is positive, and stabilizing when it is negative. The former result echoes previous findings on metapopulation stability [20, 13, 25, 24]. The latter indicates that positive density-dependence is stabilizing in populations facing high pressures on production, which could help understand why this behavior is widespread in birds and mammals [16].

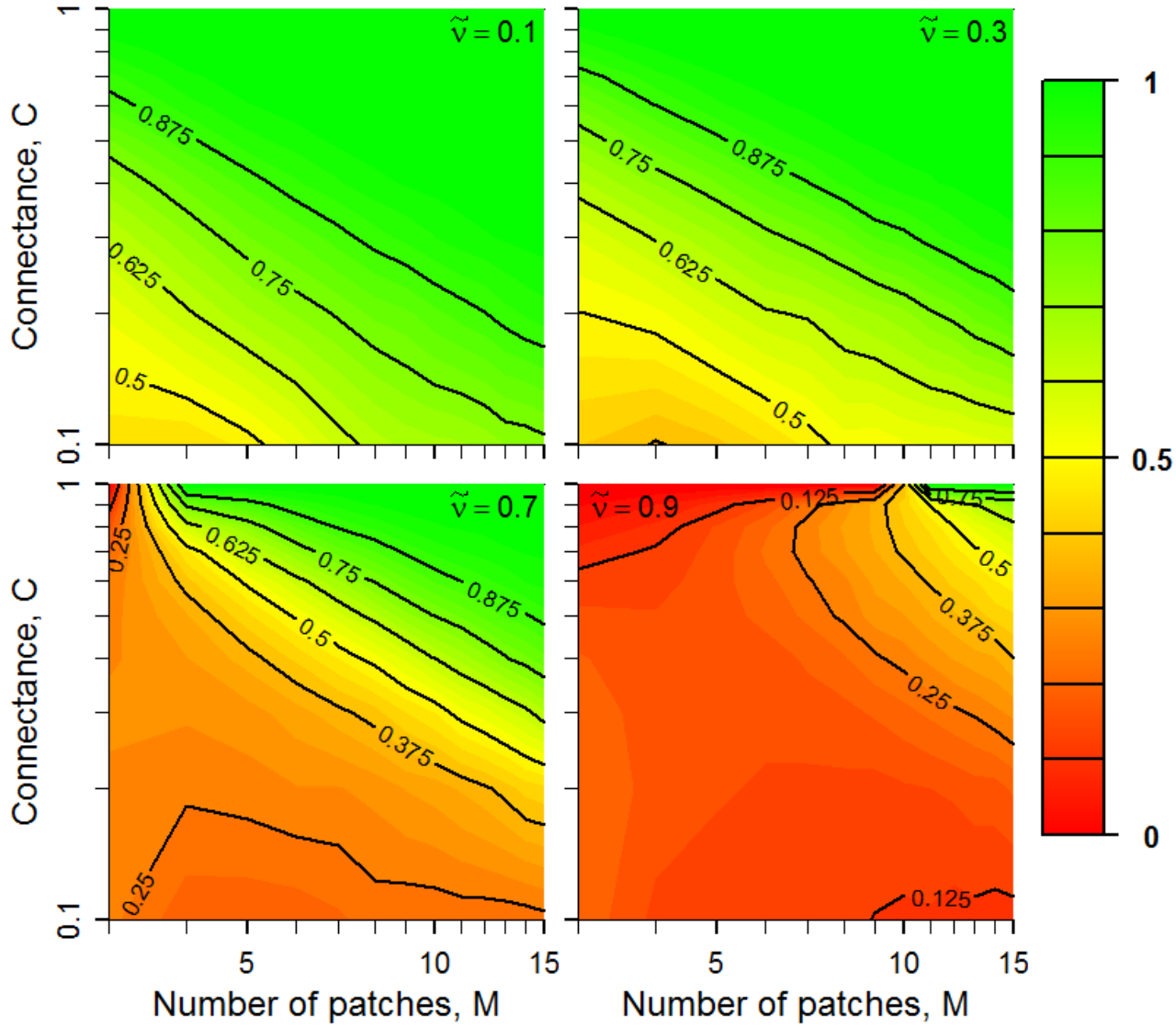


Figure 2: Dependence of the impact of dispersal on stability on the number of patches M and the connectance C, for heterogeneous patches. Proportion of webs for which migration is stabilizing (PSD) is shown, in dependence on the log of M and the log of C. Each panel corresponds to a different fraction of growth due to dispersal $\tilde{\nu}$. Upper-left panel: $\tilde{\nu} = 0.1$; upper-right panel: $\tilde{\nu} = 0.3$; down-left panel : $\tilde{\nu} = 0.7$; down-right panel : $\tilde{\nu} = 0.9$. Warmer colors indicate a less stabilizing dispersal. Migration is stabilizing for low $\tilde{\nu}$ and high C and M. When $\tilde{\nu}$ is high, dispersal is less stabilizing in small and highly connected networks, and in large and poorly connected networks.

Table 3: Comparison of the results with the existing litterature

Dispersal behavior	Effect on stability		
	Stabilizing	Destabilizing	No effect
Homogeneous metapopulation			
Density-independence ($\omega = 1$, $\zeta = 0$)		Bascompte & Solé (1994) **Our model when modified (see Conclusions)**	Hassel *et al.* (1995) Rohani (1996) Jang & Mitra (2000) Jansen & Lloyd (2000) **Our model (for all ϕ)**
Positive density-dependence ($\omega > 1$, $\zeta = 0$)	**Our model ($\phi < 0$)**	Ruxton (1996) Jang & Mitra (2000) Silva *et al.* (2001) Silva & Giordani (2006) **Our model ($\phi > 0$)**	
Costly dispersal ($\omega < 1$, $\zeta = 0$)	Ruxton *et al.* (1997a) Ruxton *et al.* (1997b) Stone & Hart (1999) **Our model ($\phi > 0$)**	Kisdi (2010) **Our model ($\phi < 0$)**	
Social fence ($\omega = 1$, $\zeta < 0$)	Stenseth (1988) **Our model ($\phi > 0$)**	Hestbeck (1982) **Our model ($\phi < 0$)**	
Settlement facilitation ($\omega = 1$, $\zeta > 0$)	**Our model ($\phi < 0$)**	**Our model ($\phi > 0$)**	
Heterogeneous metapopulation			
Density-independence ($\omega = 1$, $\zeta = 0$)	**Our model** (low dispersal and high complexity)	**Our model** (high dispersal, and small highly connected networks or large poorly connected networks)	Dey *et al.* (2006)

Third, we found that a costly dispersal is stabilizing when the sensitivity of production to density is positive. It has already been suggested that costly dispersal can stabilize metapopulations [22, 21, 27], but Kisdi (2010) showed that costly migration can also be destabilizing under certain conditions, depending on the properties of local patches dynamics [14]. We indeed found that costly dispersal is destabilizing when the sensitivity of production to density is negative.

Fourth, we showed that a social fence is destabilizing when the sensitivity of production to density is negative, and stabilizing when it is positive. The former result echoes Hestbeck's assumption that a social fence induces oscillations and thus destabilize the system [12], whereas the latter is coherent with Stenseth's advocacy of a stabilizing effect of a social fence [26]. Our model conciliates those results, by showing that the impact of a social fence on stability depends on local population dynamics.

Fifth, we suggested that settlement facilitation towards immigrants is stabilizing when the sensitivity of production to density is negative, and destabilizing when it is positive. Evidence shows that settlement facilitation is widespread among marine organisms, and can occur through a modification of the environment [1]. Note that we do not evoke conspecific attraction, which has widely been studied experimentally [23]. A conspecific attraction would indeed mean a sensitivity of emigration to the recipient patch, whereas our model focuses on immigration.

Sixth, we showed that in heterogeneous metapopulations, density-independent dispersal can have an influence on stability. It contradicts the suggestion that metapopulation models are robust to spatial heterogeneity of demographic parameters [3]. Further, we found that the importance of immigration in population growth and the topology of the metapopulation network modify the impact of dispersal on stability. Dispersal is more stabilizing in complex networks, whereas it is less stabilizing in small and poorly connected webs.

In this paper, we showed that dispersal can impact metapopulation stability through various dispersal behaviors, and that the effect of these behaviors on stability crucially depends on the local within-patches dynamics of the metapopulation. We also suggested that in more realistic heterogeneous metapopulations, dispersal can yield an effect on stability through the sole topology of the metapopulation network. Further work could be done to elucidate the precise spatial patterns enabling a stabilizing dispersal, in relation to within- and between-patches dynamics.

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